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Marine Snails of the Genus *Phorcus*: Biology and Ecology of Sentinel Species for Human Impacts on the Rocky Shores

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Additional information is available at the end of the chapter

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Abstract

In this review article, the authors explore a broad spectrum of subjects associated to marine snails of the genus *Phorcus* Risso, 1826, namely, distribution, habitat, behaviour and life history traits, and the consequences of anthropological impacts, such as fisheries, pollution, and climate changes, on these species. This work focuses on discussing the ecological importance of these sentinel species and their interactions in the rocky shores as well as the anthropogenic impacts to which they are subjected. One of the main anthropogenic stresses that affect *Phorcus* species is fisheries. Topshell harvesting is recognized as occurring since prehistoric times and has evolved through time from a subsistence to commercial exploitation level. However, there is a gap of information concerning these species that hinders stock assessment and management required for sustainable exploitation. Additionally, these keystone species are useful tools in assessing coastal habitat quality, due to their eco-biological features. Contamination of these species with heavy metals carries serious risk for animal and human health due to their potential of biomagnification in the food chain. Thus, the use of these species as bioindicators is warranted to the establishment of conservation measures targeting marine coastal environments. Climate change increases the level of environmental stress to which intertidal organisms are subjected to, affecting the functioning of biological systems at different levels of organization. *Phorcus* species have been widely used as indicators of the effect of climate change on local disturbances of intertidal ecosystems and geographic distribution shifts of these organisms. Further studies concerning biological parameters of *Phorcus* species and how they react to exploitation, pollution, and climate change will consolidate these species as indicators of large-scale ecological impacts of anthropogenic activities.

Keywords: *Phorcus*, topshells, life history traits, fisheries, pollution, climate change

1. Introduction

Topshells are marine gastropods that inhabit the rocky shores. These marine snails together with limpets and winkles are the most successful algal grazers present in the intertidal of the Northeastern Atlantic and Mediterranean Sea [1]. Topshells occupy the rocky sea shores from the supratidal to the subtidal, one of the most extreme, heterogeneous, and dynamic environments in nature that expose these organisms to different levels of thermal and hydric stresses [2, 3]. These unpredictable environmental conditions are therefore responsible for many of their peculiar morphological and biological characteristics that can be perceived as adaptations to the intertidal environment [4]. The marine snails of the genus *Phorcus* are ecologically important algae grazers that play a major role in regulating the ecological balance of their habitat and have often been used as biological indicators in evaluating the consequences of anthropogenic impact on this ecosystem [4, 5].

The diversity and ecological importance of the genus *Phorcus* prompted intensive research over the past years. Recently, this genus was redefined by Donald et al. [5] to include species previously under the genus *Monodonta* Lamarck, 1799, or *Osilinus* Philippi, 1847, allowing to trace the biogeographic history of this genus' origin to 40–20 Ma, prior to the closure of the Tethyan Seaway.

Intertidal invertebrates' life history traits vary inter- and intraspecifically because of genetic differences and environmental effects. Growth, reproductive strategy, and mortality depend on a complex combination of selective forces and are fundamental to understand the distribution and abundance of these species along the intertidal [6, 7]. As such, knowledge of life history traits of *Phorcus* populations provides important information required to understand how these species adapt to an ever-changing environment, whether because of human activities, such as fisheries, habitat disturbance, pollution and climate change, or natural causes.

One of the main causes of disturbance in the intertidal ecosystem is the harvest of gastropods in the rocky shores, which has occurred since prehistorical times, resulting in shifts in abundance and/or size structure of these species. Another cause of disturbance is the contamination of coastal waters, by the presence of unnatural chemicals, as a result of industrial spillage and sewage discharges among others. Gastropod molluscs are frequently used as bioindicators to assess the health status of the coast and determine the effect of marine pollution [8]. Walsh et al. [9] recorded that these sentinel species have the potential to act as a useful biomonitoring system of pollutants in the marine environment. As such, they act as pollution indicators by tracing metals, providing information required for the establishment of protective measures of the ecosystem.

Phorcus species are recognized as good bioindicators of water quality due to their reduced mobility, easy sampling, adequate size for tissue analysis, widespread distribution, abundance all year-round, and ability to accumulate high metal concentration in their shell and tissues, reflecting heavy metal availability in coastal waters [10, 11].

Global climate change also causes disturbance in the intertidal ecosystem that results in changes in the geographical distribution of marine gastropods. Intertidal invertebrates are

known to respond to climate change through alterations in biogeographic distributions following a latitudinal gradient, from warmer towards cooler regions. *Phorcus* species are bioindicators and changes in their distribution have been successfully linked to hypothesis of climate change on Northeastern Atlantic shores, particularly in species presently at their northern limits, which may be expected to move further north as the coastal waters continue to warm, as has happened in the last decades.

The aim of this work is to compile and review a wide array of subjects related to *Phorcus* species biology and ecology, comprising anatomy, growth, reproduction, mortality, behaviour, and ecological role and also to evaluate and discuss the consequences of anthropological impacts such as fisheries, pollution, and climate changes on these keystone species and their potential as bioindicators of the effect of human activities on coastal marine environments.

2. Biology and ecology of topshells

2.1. Anatomy

Gastropods are comprised essentially of two main parts: the shell and the body. These asymmetrical molluscs have a twisted, spirally coiled shell around its body, which protects them from biotic and abiotic factors present in their environment, and a corneous or calcareous operculum, a flat plate that rests on the upper dorsal side of the foot that acts as a supporting pad for the shell. When the snail actively moves or blocks the aperture, the body withdraws, protecting the animal from predators and preventing water leakage in exposed rocky shores [12, 13].

In topshells, the shell is complete and usually pyramidal, moderately large, conical to globose in shape, with rounded to angular body whorls and often with a flattened base and an interior consisting of mother-of-pearl. This structure is formed in the embryonic stage, with the secretion of protein fibres from the outer skin of the visceral mass and from the mantle, while they are free-swimming larvae and they are followed by the secretion of calcium carbonate from the same cells. Posterior to the embryonic phase, the shell continues to grow through the addition of a protein mesh and calcium carbonate mostly on its margins but also on its interior. Shell growth is not continuous and it frequently leaves different growth lines since maturity and adverse environmental conditions may cease growth. The shell offers refuge both from predators and from desiccation being impervious to gasses and liquids and resistant to crushing [12–14]. Colour patterns of the shell are usually highly variable in topshells and are mostly related to diet rather than to genetic control (**Figure 1**) [12].

The soft body consists of two compartments connected by a waist and present a dark ash colour with a greenish tint [15]. The lower compartment encompasses the muscular foot and the head. The foot is used for locomotion over the substrate, swimming, jumping, and returning the animal to an upright position when overturned. Also, it helps to detect food. The upper compartment is used for respiration, digestion, excretion, gamete production, and shell secretion. The body of these organisms comprises a head with a short snout, a pair of conical



Figure 1. Shell phenotypic variability of *Phorcus sauciatus*. A – Portugal mainland, B – Madeira Island, C – Gran Canaria Island.

and papillate tentacles, cup-shaped open eyes on distinct stalks, a foot, a muscular ventral organ with a flattened base used for locomotion, and a visceral mass, which fills dorsally the spire of the shell and contains most organ systems and the mantle, a collar-like tegument, which lines and secretes the shell, and forms a mantle cavity normally provided with respiratory gills for breathing in water and a well-vascularised mantle cavity, which allows the animals to breathe in air [13, 14].

2.2. Taxonomy and geographic distribution

Phorcus Risso, 1826, are herbivorous marine snails (Gastropoda: Prosobranchia) belonging to the family Trochidae Rafinesque, 1815, that inhabit rocky shores from the Mediterranean Sea through the Northeastern Atlantic Ocean including the Macaronesian Archipelagos of Madeira, Canaries, Azores, and Cape Verde [14].

This genus of gastropod grazers is currently represented by nine recognized living species [5, 6] and is comprised of *Phorcus articulatus* (Lamarck, 1822), *Phorcus atratus* (Wood, 1828), *Phorcus lineatus* (da Costa, 1778), *Phorcus mariae* Templado & Rolán, 2012, *Phorcus mutabilis* (Philippi, 1851), *Phorcus punctulatus* (Lamarck, 1822), *Phorcus richardi* (Payraudeau, 1826), *Phorcus sauciatus* (Koch, 1845), and *Phorcus turbinatus* (Born, 1778) [1, 5].

There is a clear separation between the species of *Phorcus* that occur in the Atlantic and the Mediterranean. This split distribution is thought to result from the barrier imposed by the Strait of Gibraltar, since there is no species overlap in the adjacent area, and the nearby Alboran front that act as biogeographic breaks for animals with short larval stages, such as *P. lineatus*, whose lecithotrophic veliger larvae remain in the water column for, at the most, 6–7 days [5, 14, 16]. As such, four species of this genus are restricted to the Mediterranean Sea, specifically *P. turbinatus*, *P. mutabilis*, *P. articulatus* and *P. richardi* and the remaining five species occur in the Northeastern Atlantic Ocean, namely *P. lineatus*, *P. sauciatus*, *P. atratus*, *P. punctulatus*, and *P. mariae* (Figure 2) [5].

In the North Atlantic Ocean, *P. lineatus* is the species that reaches the northernmost geographic limits of the genus *Phorcus* in North Wales and Ireland and *P. punctulatus* the southernmost limits in Senegal. *P. mariae* is restricted to Cape Verde archipelago, *P. atratus* to the Canaries archipelago and Selvagens Islands, and *P. punctulatus* to Senegal [1, 5, 14]. *P. lineatus* has a wide distribution ranging from North Wales and Ireland to Morocco and *P. sauciatus* includes

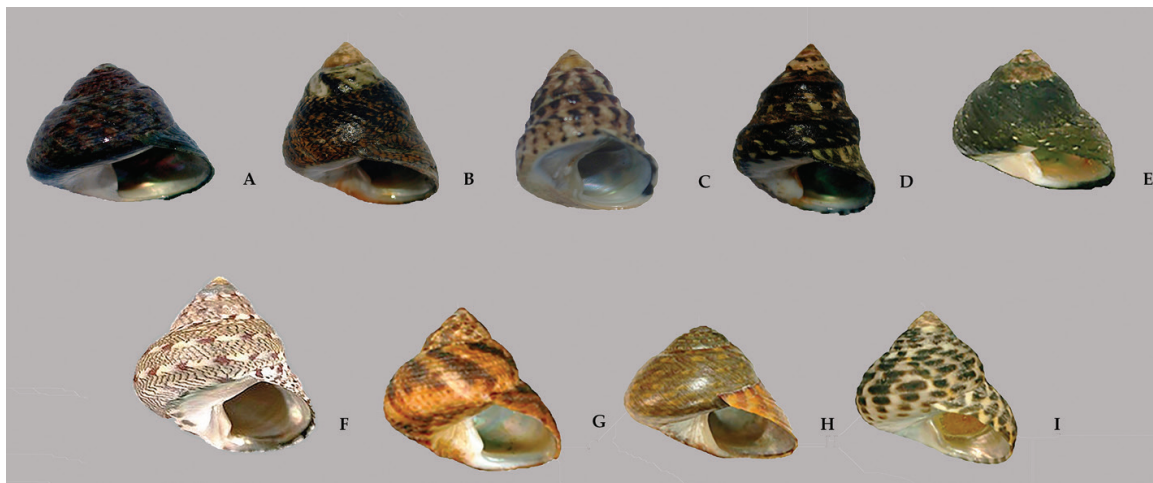


Figure 2. Shells of the nine species of the genus *Phorcus*. A – *Phorcus sauciatus* from Madeira archipelago, B – *Phorcus lineatus* from mainland Portugal, C – *Phorcus atratus* from Selvagens Islands, D – *Phorcus mariae* from Cape Verde archipelago, E – *Phorcus punctulatus* from Senegal (NMR 36429) [17], F – *Phorcus articulatus* from Spain (NMR 36447) [17], G – *Phorcus mutabilis* from Greece (NMR 36658) [17], H – *Phorcus richardi* from Greece (NMR 36669) [17], I – *Phorcus turbinatus* from Greece (NMR 36606) [17]. Images E, F, G, H, and I by Joop Trausel and Frans Slieker and available online at NMR – Natural History Museum Rotterdam [17].

the Macaronesian archipelagos of Madeira, Canary, and Azores with its northern boundary in the Iberian Peninsula and its southern limit in the African mainland, with negligible genetic differentiation between them, suggesting either recent or continuing dispersal among these areas [5, 18, 19].

Concerning the geographic distribution of the genus *Phorcus* in the Mediterranean Sea, *P. turbinatus* occurs from Spain to Cyprus, *P. articulatus* from Spain to Tunisia, *P. richardi* from Spain to Croatia, and *P. mutabilis* from Italy to Turkey [5].

Topshells as limpets are subject to an array of environmental stresses due to their extended vertical distribution, which ranges from the upper to the lower shore levels. Thus, these organisms can exhibit varying degrees of structural adaptations since their position relative to the shore influences their exposure to desiccation, hydrodynamic action of the waves, temperature variation, and tidal width [20–23], resulting in a wide array of intraspecific phenotypic variability.

2.3. Respiratory system

Marine snails of the genus *Phorcus* have a gill for water breathing and a well-vascularised mantle cavity, which allows the animal to breathe in the air [14]. The mantle cavity placed between the body and its overhanging mantle skirt is constituted by a single gill in the front part of the mantle cavity and thin-walled organs that absorb oxygen from the sea water [12].

The marine snails' blood, the haemolymph, contains haemocyanin, a copper-containing protein that can fix and transport two to three times more oxygen, from the gills to the heart, than organisms without this protein. The heart pulsations push the oxygen-rich blood over a closed system of arteries that lead the blood to a system of open arteries, without epithelial

walls, that surround the viscera and the muscles covering all organs with oxygen-rich blood. The body organs receive the oxygen from the haemolymph and release carbon dioxide into it, which then returns to the gills, via a system of veins, where it releases the carbon dioxide and again receives oxygen [12].

2.4. Feeding habits, behaviour, and ecological importance

Molluscan grazers are known to have an important influence on the overall structure of benthic marine communities, because of the influence and control they exert on algae [24, 25]. Removal of grazers often leads to an imbalance on the population dynamics of the species involved on the rocky shores ecosystem, due to a dramatic development of seaweed beds [25].

Topshells, winkles, and limpets form a guild of microphagous herbivores that feed on microbial biofilms, by grazing the rocky substrate with the radula, a specialized rasping organ unique to molluscs, on which successive rows upon rows of backwards-pointing teeth are placed. The teeth crack, break, and wear away during use, by the food or the hard substrate from which the sea snail scrapes [12]. Marine snails can all be found together, grazing on the open shore, and it is probable that these various snail species do not feed in exactly the same place, at the same time, in the same manner, or on exactly the same food [14] in order to avoid interspecific competition. The feeding adaptations between these species can be behavioural through spatial differentiation or anatomical through adaptations in the radula. Among these species, radulae show different hardness and patterns, being multi-fine-toothed rhipidoglossan in topshells, less complex taenioglossan in winkles, and simple docoglossan in patellid limpets; therefore, it is easy to conclude they feed in different ways [14].

In several species of sea snails, the digestive fluids contain the cellulase enzyme that breaks down cellulose. This is one of the very few cases throughout the animal kingdom of an animal producing an enzyme capable of breaking down cellulose [12]. Feeding behaviour in topshells is assumed to occur at night or during high tide as stated by Crothers [14] for *P. lineatus*. Food particles are gathered by the radula, squashed by the jaws, and then transported inward into the mouth where the digestive track begins, in the front of the body, and then transported back along the body through the oesophagus to the stomach where most of digestion occurs, and finally, digested food loops and descends forwards to the intestine where faeces are formed and expelled by the anus, which drains into the mantle cavity, at the front of the body [12].

Common topshells and edible winkles swing their head from side to side while crawling and may leave grazing tracks on the rock surface and visible slime trails. Usually, the more active species secrete a thicker layer on which to crawl and this may show up as a pale band over the rock surface. Trail-following, namely the crawling over existing mucus trails, will reduce the expense of producing a mucus trail. These trails might also be used to locomote back home, to find mates, and to assist in feeding, by trapping food particles from the water column [12]. Marine snails crawl by squeezing the front end of the foot against the substrate and by means of a ripple of muscle contraction, pass that point of contact forcing the mass of the snail forwards. In topshells, the two halves of the foot work independently of each other, out of phase, producing a characteristic slime trail [26].

Contrary to limpets, topshells are active at low tide and respond very rapidly to changes in weather conditions, moving out into the open when the sun shines and hiding from rain or cold winds in crevices or under boulders [26]. These species are limited in their vertical zonation by their tolerance to temperature variation; as such, they undertake vertical migrations up and down the shore over the seasons [27].

Wave action also acts as a limiting factor on suspension feeders and on semisessile and sessile organisms that are favoured on exposed conditions, since the water movement allows the flow of food, propagules, nutrients, and preys to these organisms. However, in these habitats, the increase of exposure to wave action involves an increase on the risk of dislodgement and physical damage, limiting the range of susceptible and physically fragile species [2]. In order to overcome the adverse conditions of the exposed areas, intertidal gastropods inhabiting these areas have a thin and smooth shell with large aperture due to the large foot required to cope with the higher risk of wave displacement and to be able to maintain a firm hold on rocky surfaces [28, 29]. In dangerous circumstances, a snail withdraws into its shell and adheres firmly to the substrate, so as to not be detached by waves or predators [12]. In the Northeastern Atlantic, *P. lineatus* is usually used as an indicator of sheltered rocky shores [30] contrary to *P. sauciatus* that seems to be more tolerant to wave action being found lower on the shore but also able to establish on sheltered zones [18]. The anatomic features of these two species corroborate this hypothesis since *P. sauciatus*' thinner shell, larger foot, and consequently large aperture imply that this species is more tolerant to wave action than *P. lineatus* with thicker shell and smaller aperture. On the other hand, these anatomic differences result in *P. sauciatus* being less tolerant to desiccation than *P. lineatus*.

2.5. Growth

Growth is a key variable in determining the survivability of any given animal, and it is important to understand the factors that drive it [31]. Biological parameters such as growth rate, asymptotic length, longevity, and age structure reflect the overall state of health of a population and are commonly used as stock assessment tools of exploited marine organisms [4]. In gastropods, growth rates have been determined through several features such as growth lines and rings in shells [32, 33], opercula [34], and statoliths [35]. Size and age of topshells are positively related, thus allowing to investigate population structure [36].

Size and growth rates in the species of the genus *Phorcus* are influenced by fluctuations in food supply [26, 37], competition [38], and wave action [39], while population density is mainly controlled by the successful settlement of larvae and predation [26, 38]. The oceanographic current systems are known to be largely responsible for the water temperature and nutrients of the coastal ecosystems, which mark the distribution and behaviour of organisms throughout the coastlines [2]. As such, temperature also influences growth in the species of the genus *Phorcus*. For instance, Crothers [14] and Mannino et al. [40] observed that a decrease in water temperature promotes a metabolic deceleration, resulting in the interruption of growth during the winter in *P. lineatus*. However, after this season, growth continues rapidly through the year, slowing only in the next winter. In general, in the first year, the growth rate of this species is high and decreases thereafter [14] as a possible result of achieving sexual maturity.

In the first six months postsettlement, specimens can grow up to 8 mm diameter, reaching 11–15 mm by the end of the year [41]. Although the growth rates slow down dramatically after the achievement of sexual maturity, since energy is mostly directed towards reproduction, growth continues throughout the life cycle of this species. In habitats with low abundance, *P. lineatus* grows rapidly to a large size and reaches maturity early but has lower longevity. While individuals that live in habitats where they are more abundant grow slowly, they do not achieve great size and may live to an older age. These differences in growth are likely related to different levels of food availability depending on population density, which in turn is related to settlement success and predation evasion [26]. The specimens of this species have been known to reach a size of 34 mm in shell height and a longevity of 15 years of age in southern Britain [36]. *P. sauciatus* have approximately the same size range of *P. lineatus*. For instance, in the Madeira archipelago, *P. sauciatus* size ranges from 2 to 28 mm (pers. obs.); in the Canary Islands, this species size ranges from 5 to 26 mm [42]; and in the Portuguese mainland coast, its size ranges from 7 to 24 mm (pers. obs.). There is, however, a great gap in knowledge concerning life history parameters of *Phorcus* species. Most studies focused on *P. lineatus* due to their wide geographical distribution spanning from Morocco to North Wales/Ireland. Life history parameters such as growth rates, asymptotical length, size at first maturity, recruitment patterns, and mortality of *Phorcus* species are likely to differ inter- and intra-specifically as a result of different biotic and abiotic factors. Further studies on the biology and population dynamics of *Phorcus* are therefore required in order to guarantee the implementation of successful conservation strategies and a sustainable exploitation based on effective management measures.

2.6. Reproduction

Topshells' reproductive system is usually strikingly simple, with a genital duct opening into the mantle cavity through the right kidney. Sea snails commonly have separate sexes but these species are not externally sexually dimorphic and sex determination is only possible through macroscopic observation of the gonads. Internally, the most reliable character for sorting them is the appearance of the urogenital aperture. In males, the lips of this organ are unpigmented and smaller, while in females, the lips are yellow and swollen. Nevertheless, in the ripe state, males have cream testis and females greyish-green ovary covering the digestive gland and viscera [43, 44], being therefore easily differentiated in the breeding state. The lobes of the gonad, whether ovary or testis, lie near the apex of the visceral hump, among the lobes of the digestive tube, and they drain into the pericardium [12].

Prior to the breeding season, adults migrate up shore to the high eulittoral zone. It seems that this migration brings the animals into a region of higher temperature required for spawning. An increase in temperature may stimulate spawning as suggested by Desai [44] who observed that adults that have migrated furthest up shore were the first to spawn.

In fact, spawning in intertidal organisms seems to be promoted by environmental triggers such as temperature, high wind speed, and wave action. Biological factors as an increase in phytoplankton concentration may also stimulate spawning as occurs in limpets [38, 45]. As such, breeding stages of a given species may differ according to their geographical position. In fact, in

the northernmost range limit, breeding seasons are shorter with a single spawning period, while in southern regions, the breeding season is longer with multiple spawning events [46, 47]. For instance, in *P. lineatus* from Asturias, Spain, the gonadal development occurs from November to June and the breeding stages from June to September and may last until November in some specimens [46]. Spawning occurs between May and August [48]. Further north in Wales, the same species is reported to have a shorter spawning season, lasting from July to August [14]. On the other hand, *P. turbinatus* that occurs in the Mediterranean Sea appears to have a longer breeding period with two spawning events in spring and autumn [49].

Fertilisation is external, with both sexes releasing their gametes into the sea and the whole process occurs directly in the water. During the reproductive season, males and females approach each other and then females send out chemical signals, leading to sperm being discharged in the water by males, which in turn stimulates females to release the oocytes [12]. According to Desai [44], males discharge clouds of spermatozoa that become very active 2 or 3 minutes after being released, and females liberate oocytes separately, a few at each spasm. This process of external fertilisation, regarded as a primitive trait in snails, becomes a high-risk strategy and improbable to succeed unless the species is locally common [14]. The fertilised egg develops within approximately a day and becomes trochophore larvae, which are capable of independent locomotion. The veliger larvae enclosed in a tiny shell develop in one or two days. At metamorphosis, the veliger turns upside down with the foot becoming ventral and the shell dorsal. Posterior to the snail's development, the back dorsal rotates in 180° anticlockwise in relation to the head and foot. Veliger larvae remain in the water column for at most 6–7 days [5, 14, 16], and at settlement, the shell measures a little over 1 mm across [14]. According to Heller [12], the trochophores of the genus *Phorcus* hatch down shore, within approximately one day and the veliger settles 4–5 days with about 1 mm. For *P. lineatus* in the United Kingdom, the recruits achieve 5–6 mm shell length by the first autumn and are detected on the bare rock between September and November and recognized, with 6–14 mm, through their first year [33].

The gap in size at settlement and size at first capture reported for topshells may be understood as a potential argument for the existence of nursery areas, underneath boulders or fissures, in which small juveniles are much commoner, but there appears to be no uniform pattern [14]. For instance, in Madeira archipelago, the juveniles of *P. sauciatus* are commonly found under boulders, with the smallest individuals having 2 mm in diameter (pers. obs.). These boulders may function as a nursery for topshell juveniles as they provide protection against abiotic factors, such as wave action and desiccation, and biotic factors, such as predation and substrate competition.

3. Anthropogenic impacts on the genus *Phorcus*

3.1. Harvesting

Intertidal and shallow-water grazers are extremely vulnerable organisms because of their limited habitat and their accessibility to human activity [50]. Hunter-gatherers have exploited intertidal grazers, since prehistoric times, and there are evidences that the densities and the

maximum sizes of several species were reduced by the exploitation [51, 52]. Studies performed in Northern Spain showed that topshells and limpets were collected, at subsistence exploitation levels, from intertidal areas of exposed shores, leading to the formation of huge shell middens [53]. In fact, intertidal resources have always been collected by humans as food supplement or used as a bargaining chip with other products worldwide [54, 55].

Several studies were carried out aiming to investigate the temporal patterns of worldwide topshell exploitation. A proven approach to study these temporal patterns of prehistoric shellfish exploitation is the analysis of the oxygen isotopic ratio ($\delta^{18}\text{O}$) of the latest growth increment of mollusc shells [56, 57]. Variations in oxygen isotope ratios from shell carbonates are mostly dependent on sea surface temperature (SST), which enables the estimation of temperatures during periods of shell growth and helps to determine the season of the year when the mollusc died [58]. Colonese et al. [59] applied this approach to the topshell *P. turbinatus* from archaeological sites in Italy and concluded that Mesolithic *P. turbinatus* exploitation was carried out almost exclusively during the colder and intermediary seasons, with very sporadic harvesting during the warmer seasons.

The same approach has been followed by Gutiérrez-Zugasti et al. [58] that confirmed the potential of oxygen isotope analysis on *P. lineatus* for paleoclimate reconstruction and also showed that the aragonite of those shells grew under conditions of isotopic equilibrium, opening new avenues for future research. This species is commonly found in Holocene archaeological deposits of Atlantic Europe and is one of the most abundant subsistence resources utilized during the Mesolithic in northern Spain.

Continued exploitation of these species is likely to incur in shifts on size and shape over time. Colonese et al. [59] observed a significant change in shell shape of *P. turbinatus*, with slender Mesolithic shells being replaced by squatter forms in the Meso-Neolithic. These differences were explained with collection shifting from sheltered shores in the Mesolithic to exposed rocky shores in the Meso-Neolithic, thus confirming the potential effect of human collection on size and shape of this exploited species.

In recent times, however, the pattern of exploitation has changed both quantitatively and qualitatively, due to the expansion of human population, to the commercial value of several species and to the industrial development that facilitated shipping and flying products around the world [25]. Limpets, abalones, chitons, winkles, and topshells are common gastropods of intertidal rocky shores; however, some species are in serious decline mainly as a consequence of overexploitation [60]. The exploitation of these resources has plentiful direct and indirect effects on the trophic chains of marine ecosystems, with potential complex cascading effects [61].

The direct effects of exploitation are the decline of the exploited species' abundance and a shift in size composition of their populations that results from the size-selective nature of harvest. Ramírez et al. [42] assessed the effects of human impacts over the abundance and size patterns of topshells (*P. atratus* and *P. sauciatus*) and limpets (*Patella aspera* Röding, 1798, *Patella candei* d'Orbigny, 1840, and *Patella rustica* Linnaeus, 1758), usually collected in the Canaries archipelago. The authors observed significant differences in size structure of these

species among islands, according to the level of human influence and verified that not only all large-sized individuals disappeared from the most populated island, but also that there was a decrease in numbers for the majority of size ranges, concluding that the observed differences among islands were mainly a consequence of the human activities. In fact, in exploited populations of broadcast spawners such as topshells and limpets, the decrease of larger individuals will reduce the reproductive success leading to a decrease in population abundance and, in extremes cases, conduct to the disappearance of the species [62, 63].

Also, differences on spatial distribution of the abundance and biomass of *P. articulatus* were observed by Cheour et al. [64] along the coast of Tunisia. The authors concluded that these differences were related to several anthropogenic and environmental factors.

Even though species of the genus *Phorcus* have been exploited by humans since prehistoric times, information regarding the status of exploited stocks is scarce and exploitation is generally unregulated. Recently, some efforts have been undertaken in the Canaries archipelago, aiming to contribute to the recovery of the stock of *P. sauciatus* and *P. atratus* in a short and medium term, namely by implementing a minimum capture size of 15 mm of shell longitude for both species [65].

Overexploitation of marine organisms prompts the implementation of management policies in order to protect the exploited populations and mitigate human impacts. Currently, protection of *Phorcus* species is mostly guaranteed by the implemented marine protected areas (MPAs); however, further measures should be equated especially in regions where exploitation of these species is more intensive. Management measures and regulation aiming at a sustainable exploitation of these species are therefore warranted, as is the improvement in enforcement of existing legislation and involvement of all interested stakeholders; otherwise, protection of topshells will remain ineffective.

3.3.1. Harvest of *Phorcus sauciatus* in the Madeira archipelago: an historical perspective

P. sauciatus is the most abundant of the two species of the genus *Phorcus* described for the Madeira archipelago and has a wide geographical distribution, occurring in all islands including Madeira, Porto Santo, Desertas, and Selvagens. *P. atratus* is also present in this archipelago as the endemic subspecies *Phorcus atratus selvagensis* restricted to the Selvagens Islands. However, according to Donald et al. [5], the classification of this subspecies needs additional clarification.

P. sauciatus is harvested in the Madeira archipelago since early colonization times, remounting back to the beginning of the fifteenth century. According to Silva and Menezes [66], *P. sauciatus*, formerly identified as *Trochus colubrinus* Gould, 1849, occurred in the intertidal zone of all the islands and was consumed salted or pickled, being imported from the Selvagens Islands in a relatively large quantity. This species was also used as bait for fisheries.

Nowadays, *P. sauciatus* continues to be caught in Madeira and Porto Santo, except in marine protected areas, without harvest regulation or auction obligation. The harvest of this species in the Madeira archipelago became more intensive due to the development of their commercial

exploitation supported by technological advances in methods of collection, processing, storage, and transportation, but also due to the increase in human population density and the accessibility to the coastal zones. As such, shifts in abundance and/or size structure of this species occurred mainly in the south coast of Madeira Island, resulting in a reduction in abundance levels and sizes of the caught specimens, due to the existence of more favourable environmental conditions, higher population density, and easier accessibility.

Given the current scenario, it has become vital to know the biological and ecological traits of *P. sauciatus* in Madeira archipelago and its population dynamics. As such, the Fisheries Research Service from the Regional Directorate of Fisheries of the Autonomous Region of Madeira presently develops a full study on this species aiming to establish proper conservation strategies, in order to preserve this important keystone resource of the intertidal zone, that would contribute towards the reduction of the risks of overexploitation and promotion of a sustainable harvest of *P. sauciatus* in the Madeira archipelago, through the implementation of suitable regulation and management measures considering the biological and ecological specificities of this species in this region. At a first glance, the implementation of regulation concerning harvest techniques, maximum allowable catch weight, and minimum catch size should be considered and also mandatory landings. Depending on the results obtained in the study, other measures might have to be pursued in order to provide an adequate management for a sustainable exploitation of this resource such as the establishment of a closed season to ensure optimal reproductive success.

3.2. Pollution: topshells as bioindicators of habitat health

The ecological effects of increasing levels of heavy metal concentrations in the environment are of great concern due to their high bioaccumulative nature, persistent behaviour, and high toxicity [67].

The increase of human population and anthropogenic activities, such as the development of industry on the coastline, are the major responsible factors for pollution hot spots that occur predominantly close to major ports, industrial areas, and cities [68]. Maritime traffic also acts as a source of pollution due to the antifouling paints of boats [69]. Marine and especially coastal ecosystems are increasingly endangered by the large amounts of metal pollutants, arriving to this environment mainly by superficial runoff of rain, by direct atmospheric deposition, and by discharges from sewage effluents, spillage, and industrial establishments [70, 71]. Biological and physiological alterations in benthic communities may occur due to the toxic effects of metals and due to the sedentary lifestyle of these species [72]. Aquatic organisms can accumulate petrogenic and anthropogenic compounds such as n-alkanes, polycyclic aromatic hydrocarbons (PAHs), and polychlorinated biphenyls (PCBs) from the environment into their lipid tissues, some of which can be carcinogenic and/or highly toxic for living organisms [71]. Most of the comparative studies between taxonomic groups indicate that bioaccumulation of pollutants in molluscs is, in general, much superior than in fish [73]. Mollusc shell and tissues reflect the higher degree of environmental pollution by heavy metals and are the most useful bioindicator tools. The metal body burden in molluscs may reflect the concentrations and availability of heavy metals in the surrounding water and sediment and may thus be an

indication of the quality of the surrounding environment [74]. These organisms accumulate comparatively higher concentrations of metals, both from water and sediment, because of their sedentary nature [67].

The worldwide increase of pollution levels on coastal zones has led to the awareness of the need to perform ecotoxicological research and to define sensitive bioindicators that allow the evaluation of contamination degrees, aiming to recommend the appropriate measures to conserve the ecology of the coastal areas. The species of the genus *Phorcus* act as sentinel species due to their particular ecobiological characteristics, as abundance and wide geographical distribution, long life span, suitable dimensions, easy identification, and collection, becoming a useful biomonitoring system of pollutants in the marine environment and making these organisms suitable to measure for hazard and risk assessment. These molluscs are also sturdy enough to survive in laboratory and field studies and tolerant to environmental alterations and various contaminants [67].

P. turbinatus is generally considered as a bioindicator of metal pollution in coastal areas [69, 75], because of their ability to tolerate temperature and salinity fluctuations and survive even in hypoxia [75, 76]. Boulajfene et al. [77] evaluated the degree of metal contamination in *P. turbinatus* and monitored the impact of metals on metallothioneins functioning in the Northeastern and the Eastern coasts of Tunisia and found that sedimentological metallic contents of copper, zinc, and cadmium vary according to the area where these species live. It seems that this species has an ability to accumulate these metals and that the metal effect on protein induction may be linked to physical factors such as temperature, oxygen, and copper contents in sediment. Boucetta et al. [78] assessed the health status of *P. turbinatus* on the Algerian East coast through the analyses of the concentrations of trace metals in this species tissue and of biomarkers such as the activity of acetylcholinesterase (AChE) and glutathione-S-transferase (GST) and verified that the alteration of the activity of AChE with the induction of GST was mainly due to the presence of high concentrations of trace metals and abiotic factors including salinity and pH.

In fact, several environmental factors such as water current, water flow, renewal of water, pH, and salinity affect the distribution of heavy metals in molluscs as reported by Grupta and Singh [67]. Survival is significantly affected by salt concentration and by temperature, as well as by the interaction between them, so that the toxicities of salts are generally enhanced at higher temperatures.

Other studies support the efficacy of topshells as bioindicators, such as Bordbar et al. [79] who investigated the impact of a ferronickel smelting plant on the coastal zone of Northern Greece through the study of metal bioconcentration in *Patella caerulea* and *P. turbinatus*, concluding that the ferronickel smelting plant had heavily impacted the coastal zone. Another study on the southeast coast of Tenerife reports the use of *P. atratus* in the evaluation of the concentrations of nalkanes and PAHs in the visceral mass and demonstrated that this species is contaminated with a chronic background of aliphatic and hydrocarbons strongly retained in their lipid tissues and suggested this species as a bioindicator of petrogenic contamination [71]. Cabral-Oliveira et al. [80] presented further evidence by comparing the accumulation of trace elements in edible molluscs *Mytilus galloprovincialis* Lamarck, 1819, *Patella ulyssiponensis* Gmelin, 1791, and *P. lineatus*, between one sewage-impacted area and two reference areas in

central western coast of Portugal and suggested that the concentrations of trace elements in the soft tissues of these molluscs can be affected by the presence of sewage discharges.

Bioaccumulation of pollutants in molluscs is, in general, much superior than in fish due to their sedentary nature. Thus, their shell and tissues reflect the levels of environmental pollution and are the most useful bioindicators regarding the quality of the surrounding environment. As such, there is a growing interest in the use of these marine gastropods as bioindicators, due to their ecobiological features, both in a scientific and ecosystem management perspective. This approach will contribute to the establishment of conservation measures targeting marine coastal environments. Also, all species of the genus *Phorcus* are a food source for other species; therefore, if these species are contaminated there is a potential for biomagnification in the food chain that can carry serious risks both to wildlife and human health.

3.3. Climate change effects on intertidal communities: impacts on topshells of the genus *Phorcus*

The history of earth is riddled with events that have shaped different ages, each with specific conditions that characterized them. One of these characteristics is global temperature that has oscillated numerous times over the course of earth's long history and thus shaped biodiversity throughout the ages. For instance, the change in mean temperature between the late Pleistocene (colder conditions) and the early Holocene (warmer conditions) lead to a taxa alteration between these two periods. The more abundant species adapted to cold water, such as the periwinkle *Littorina littorea* (Linnaeus, 1758) and the limpet *Patella vulgata* (Linnaeus, 1758) in the late Pleistocene, were replaced by species better suited to warmer conditions such as *P. lineatus*, *Patella depressa* Pennant, 1777, and *P. ulyssiponensis* in the Holocene [81, 82]. A similar pattern is visible today in the Cantabrian coast, with a predominance of warmer species such as *P. lineatus* and the absence of *L. littorea* [53].

Nowadays, however, global climate change is recognized as a reality, driven mostly as a direct consequence of human activity [83, 84], namely, through the cumulative postindustrial carbon emissions to the Earth's atmosphere [85]. Known consequences of climatic change in the marine environment are the increasing global temperature, perturbed regional weather patterns with increasing wind velocity and storm frequency, rising sea levels, ocean acidification, changed nutrient loads, and altered ocean circulation [86]. These and other physical consequences are affecting marine biological processes from genes to ecosystems, over scales from rock pools to ocean basins, impacting ecosystem services and threatening human food security [85]. The rates of physical change are unprecedented in some cases and biological changes are also likely to occur at a quick rate, although the resilience of organisms and ecosystems is highly variable. Biological changes founded in physiological response manifest as species range changes, invasions and extinctions, and ecosystem regime shifts [85].

Coastal ecosystems are among the most vulnerable to climate change, especially the intertidal areas, which have shown faster biogeographic changes [87, 88] than those found in terrestrial environments [89]. Long-term monitoring studies have shown that the distribution limits of the intertidal biota of hard substrates have progressed towards the poles at a rate of over 50 km per decade [88, 90, 91].

Invertebrates and seaweeds, inhabiting the intertidal, may be particularly vulnerable to fluctuating temperatures, since individuals must adapt to the extreme temperatures of both the terrestrial and marine environments [92]. Even in small spatial scales in the intertidal zone, a broad range of thermal conditions is found that may exceed the range of large latitudinal bands. Therefore, intertidal organisms are believed to be at the limit of their physiological tolerance since these organisms are sorted by zonation in which the upper limit of one species is set by physiological stress, and species replace one another moving up the shore [88, 93]. The species most tolerant to heat and desiccation live at the top of these zones [94]. Since these organisms are thought to live at the utmost extremes of their physiological tolerance limits, any changes in abiotic parameters such as temperature and air exposure time could lead to death or local extinction [95, 96].

On the other hand, these changes can also lead to the expansion of the range and distribution area of some species. Thus, intertidal ecosystems are thought to be among the first to show responses to increases in global temperatures [95, 97] and are potential environments to assess the effects of climate change [98].

Rising temperatures can result in increased thermal stress and desiccation at low tide and in latitudinal changes in species abundance and distribution. However, changes in temperature affect the rocky intertidal; for instance, rising sea levels can result in altered zonation of intertidal biota and compression on vertical engineered defences. Also, increased storm frequency can result effectively in higher levels of wave exposure, resulting in shifts in community structure, due to a replacement of grazers by filter feeders, and shifts in direction of trophic control [85].

Intertidal organisms are subject to other factors that can lead to significant physiological stress and mortality such as shifts in salinity, increased levels of siltation, and prolonged oxygen or nutrient deprivation [99–102]. These factors play an important role in reproduction and survival of these organisms and are predicted to change in the coming decades as a result of global climate change. In fact, some of these changes are believed to have already occurred as ecological impacts on coastal ecosystems [103].

A species geographic limit reflects the interactions of organisms and their environment and is likely one of the first signals of the effect of climate change on the biota of the planet [89]. Geographical range limits impose environmental stresses, such as temperature, to populations that restrict adult survival or juvenile recruitment [88, 93]. This is related to the organisms' physiological tolerance to temperature. Exceeding these tolerance limits results in the organism's death and can lead to the local extinction of a population if temperatures are extreme enough [89]. Changing climatic conditions results in shifts of geographical limits in which populations can survive and reproduce thus acting as indicators of the processes of long-term climate change [88, 89, 93].

Species of the genus *Phorcus* like other intertidal organisms are considered good indicators of the effects of climate change in marine ecosystems. For instance, *P. lineatus* has been identified as an indicator species for monitoring climate changes around the coasts of Western Europe [104] due to its extensive biogeographic distribution, ranging from North Wales and Ireland

to Morocco [5, 14]. Crothers in 1994 [33] showed evidences that this species has extended its geographical distribution range in the Bristol Channel eastwards along the Somerset coast for at least 20 km in the past 50 years and suggests that it may be still advancing. In fact, a decade after Mieszkowska et al. [105] reported that *P. lineatus* and *Gibbula umbilicalis* (da Costa 1778) have undergone North and Northeastern range extensions in Britain, with the increase in abundance of the populations and a decrease in adult size. According to Mieszkowska et al. [104], the range limits of *P. lineatus* in the British Isles have extended by up to 55 km, between the 1980s and the 2000s, even though the extremely cold winter of 1963 in the west and south of Britain [106] prompted a cold-induced mortality [107]. The recovery of these populations occurred in subsequent warmer years with breeding populations being found up to and beyond their limits before the cold spell [105]. These shifts have been synchronous throughout this geographic region, strongly suggesting that a large-scale factor such as climate is responsible for the observed changes.

The extension of northernmost geographic limits of *P. lineatus* in the Northeastern Atlantic is one among several evidences of range shifts that have been reported in recent years and is in accordance with Helmuth et al. [88] who reported that intertidal species range limits may be shifting by up to 50 km per decade.

Another possible example of geographic range extension due to climate change could be the colonization of Santa Maria Island in the Azores archipelago by *P. sauciatus* that occurred very recently, probably after 2009. The founder population has been able to recruit itself and is currently mostly constituted by specimens under 2 years of age. Presently, this species is restricted to the most occidental island of the Azores archipelago, the nearest island to the Portuguese mainland, and to the archipelagos of Madeira and Canaries where this species is well established since colonization times. According to the same authors, a successful colonization of the remaining islands of the Azores is predicted. Even though the driving forces that lead to the recent establishment of a population of this species in this island are unknown, there is a strong possibility that it is related to the increase of sea surface temperature (SST) in the Northeastern Atlantic (**Figure 3**) [108–110]. One of the determinants of successful reproduction and recruitment of *P. sauciatus*, a subtropical species, is sea surface temperature. According to Hutchins [110], subtropical species require warmer summers in order to guarantee reproductive success; as such, an increase in SST in Azorean waters could have played an important role in the successful establishment of *P. sauciatus* in Santa Maria Island.

Changes in the abundance and distribution of *P. sauciatus* could be directly or indirectly related to climate and oceanographic events that result in an increase of SST [18]. Historically, the geographic range of this species on the Northwest coast of the Iberian Peninsula is characterized by the existence of a distribution gap between southern Galicia and northern Portugal possibly related to upwelling events in the region. The first records of *P. sauciatus* having colonized, in the early years of the twenty-first century, at least partially its distribution gap were presented by Rubal et al. [18]. These authors suggested that colonization occurred from the east and north in westward and southward direction from South Galicia to North Portugal. The beginning of the expansion in the distribution of this species in South Galicia coincided with a warming in SST in the Northeastern Atlantic due to global warming [111, 112] by the end of the 1980s and early 1990s that was responsible by similar range expansion of warm

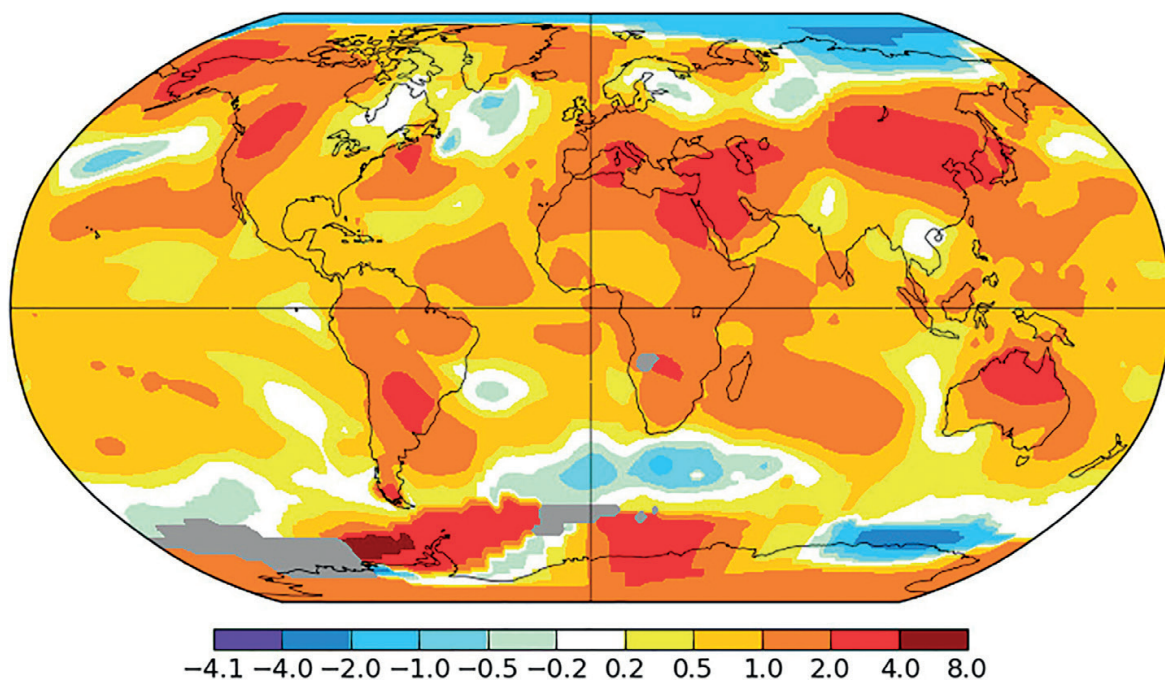


Figure 3. Map representing the spatial variability in surface warming. The temperature anomaly ($^{\circ}\text{C}$) is represented for July 2017 compared to the mean surface temperature for the period of 1951–1980 [108].

water species in the English Channel [103, 113]. Rubal et al. [18] suggest that the weakening of the upwelling since the 1940s led to an increase in SST that could have been responsible for the recent colonization of these regions by *P. sauciatus*.

These changes in oceanographic conditions could result in shifts in the distribution and abundance of *P. sauciatus* along its northern boundary; such patterns have already been reported for other gastropods in this area [114] and other *Phorcus* species at northern latitudes [104, 105].

Climate change increases the level of environmental stress to which intertidal organisms are traditionally subjected to and these may severely affect the functioning of biological systems at different levels of organization. The reviewed works of several authors provide strong evidence of the suitability of *Phorcus* species as indicators of global climate change. This is particularly true for populations in the geographic boundaries of these species that can expand up to 50 km per decade, affecting ecological interactions and community structure of the intertidal ecosystems. Alteration of vertical zonation of these assemblages is another consequence of climate change that can be inferred using *Phorcus* as indicators, since these species occur at their physiological tolerance limits. Changes in temperature, climatic patterns, and oceanographic features directly affect biological processes, which can scale up to the assemblage level, thus affecting different levels of biological organization. For instance, reduction in body size and changes in reproductive cycles are recognized as universal responses of intertidal organisms to global warming. Further studies are required in order to provide information concerning biological parameters of *Phorcus* species and how they are affected by climate change, consolidating these species as indicators of large-scale ecological impacts of climate change.

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